

A redescription of the uniquely polychromatic African cichlid fish *Tilapia guinasana* Trewavas, 1936

PETER HUMPHRY GREENWOOD

Visiting Research Fellow, Zoology Department, The Natural History Museum, Cromwell Road, London, SW7 5BD; Honorary Associate, J.L.B. Smith Institute of Ichthyology, Somerset Street, Grahamstown 6140 South Africa.

CONTENTS

Introduction	21
Methods and Materials	22
Redescription of <i>Tilapia guinasana</i>	23
Synonymy	23
Description	24
Gill-rakers	25
Scales	25
Fins	25
Oral teeth	25
Pharyngeal jaws and dentition	26
Neurocranium	27
Jaws	30
Infraorbital bones	31
Vertebral column	31
Caudal fin skeleton	31
Coloration	31
Diagnosis	32
Discussion	33
Appendix; <i>Tilapia guinasana</i> in Lake Otjikoto	36
Acknowledgements	36
References	36

SYNOPSIS. *Tilapia guinasana*, endemic to a single sink hole (surface area ca. 2800 m²) in northern Namibia, is unique amongst the species of that genus because of its extensive polychromatism, a phenomenon not recognised when the species was first described from preserved material (Trewavas, 1936). Five principal and non-sexlimited colour forms (one with several variants) are now known from this single population.

Questions have been raised about the specific status of *Tilapia guinasana*, with suggestions ranging from it being an aberrant population of the widespread *Tilapia sparrmanii* to the possibility that the different morphs represent distinct species. Recent fieldwork, and the additional material now available for detailed study, all indicate that *Tilapia guinasana* is indeed a distinct and polychromatic species with several unique morphological and anatomical features, especially osteological ones. These features are discussed and consideration is given to possible environmental influences on their phenotypic expression.

The phylogenetic relationships of the taxon remain uncertain pending a fully cladistic analysis of the genus *Tilapia*, but the derived status of the species within at least part of the genus can be established.

INTRODUCTION

Tilapia guinasana is endemic to a single sink-hole, Lake Guinas, situated in the northern part of Namibia (17°20'E, 19°19'S). Since Lake Guinas has a surface area of only ca. 2800 m², *T. guinasana* has the smallest area of endemism of any known *Tilapia* species.

At the time of its discovery by Jordan in 1931, *T. guinasana* seemed not to be present in the nearby Lake Otjikoto (17°30'E, 19°10'S; surface area ca. 4200 m²), since collections from that lake yielded only the haplochromine cichlid *Pseudocrenilabrus philander dispersus* (Trewavas). However, there are records that, in 1922, the species was introduced into Lake Otjikoto (A.J. Ribbink, pers comm., based on a letter from Mrs T. Schatz of the Tsumeb Museum) where it is

now established (together with another translocated tilapiine species, *Oreochromis mossambicus* [Peters]; see also Skelton, 1990).

The species displays a degree of colour polymorphism unique amongst tilapiine fishes, and is the only polychromatic member of its genus. That phenomenon alone makes *T. guinasana* of particular interest to both cichlid taxonomists and to evolutionary biologists, an interest enhanced by the species' limited distribution, its physical and therefore genetical isolation, its small population size, and its departure in several osteological features from its supposed nearest relative, the widely distributed *Tilapia sparrmanii* Smith.

The additional morphological, anatomical and ethological information now available, together with the well-preserved and annotated material at hand, permit a more detailed description of the species than was possible before, as well as a reconsideration of its intrageneric relationships, particularly its supposed close affinities with *T. sparrmanii* (see Trewavas, 1936) and its suggested derivation from an isolated population of that species (Penrith, 1978).

Polychromatism in *Tilapia guinasana*

In her original description of *T. guinasana*, based only on preserved specimens, Trewavas (1936) recorded the coloration as 'Uniformly blackish or particoloured; or, occasionally, with faint traces of a black band from operculum to caudal and another on upper lateral line'. Later visitors to Lake Guinas (Penrith, 1978; Skelton, 1988, 1989), however, reported the existence of several distinctive colour forms. Some of these are represented amongst Trewavas' particoloured individuals, the appearance of which matches that of recently preserved specimens whose live coloration is known (personal observations based on field-data provided by A.J. Ribbink).

The existence of such extensive polychromatism in a substratum spawning African cichlid genus otherwise characterized by '... no or minimal sexual dimorphism or dichromatism' (Trewavas, 1983: 13), and in which no examples of polychromatism have been reported, aroused the interest of Dr A.J. Ribbink. He, together with several co-workers, twice visited Lake Guinas and made detailed observations on the species (see Ribbink, Greenwood, Ribbink, Twentyman-Jones and van Zyl, 1991).

Although when viewed through the water surface the fishes appear to be either black or light blue, underwater observations revealed the presence of five principal and non-sexlimited colour forms among adult fishes, namely dark blue, olive, olive striped, blue striped, and light blue, the latter category with elements of white, light blue, yellow, and even black blotches in some individuals (Ribbink *et al.*, 1991).

Almost all juveniles less than *ca.* 25 mm standard length are greyish-green in colour, with seven or eight vertical bars and two longitudinal bands on the body. Occasionally some completely pale blue, almost white, unbarred and unbanded individuals were observed (Ribbink *et al.*, 1991).

In addition, the Ribbink party recorded, on their first visit (April, *ie.* autumn, 1988), a sixth and numerically smaller colour group which they named 'large black'. All members of this category were noticeably larger (*ca.* 127–150 mm S.L.) than those of other categories, and none was part of any breeding group observed at that time. All other colour forms were, however, represented amongst the breeding pairs (Rib-

bink *et al.*, 1991). On their second visit to the lake (October, *ie.* spring, 1989) no 'large blacks' were seen, but individuals of a comparable size (*ie.* over 120 mm S.L.), and showing three chromatic forms (dark blue, light blue and olive) were observed and seen to be members of the breeding population. Again, there appeared to be a distinct size-gap between these large fishes and other members of their respective colour morphs.

The absence of small black fishes (as seen underwater), and the apparent size-gap existing between individuals of all other colour forms and the 'large black' fishes, as well as the size-gap between the large olive, light blue and dark blue fishes and their co-morphs are phenomena that require further field and laboratory studies. There is no ethological or morphological evidence to suggest that the large specimens are members of a distinct species.

Likewise, there is no morphological evidence to suggest, as might be thought *a priori*, that the various colour morphs are distinct species. That idea is also negated by Ribbink *et al.*'s (1991) underwater observations on the pairing of different colour forms during mating. Those observations indicate that, although some morphs do show a degree of assortative mating (*ie.* like with like), this is by no means absolute and the level of inter-chromatic matings is such that the morphs of *T. guinasana* must be considered members of a single species.

METHODS AND MATERIALS

The system of external counts and measurements follows that of Trewavas (1983). Gill-raker counts are taken from the outer row of rakers on the first ceratobranchial, and exclude the single raker at the junction of that bone with its epibranchial.

The length of the keel on the lower pharyngeal bone is measured, on the bone's occlusal surface, from the anterior tip of the keel to a horizontal drawn through the point where the lateral margins of the dentigerous surface join the keel (usually at or near the first tooth or teeth of the median tooth rows). The breadth of the bone's dentigerous surface is measured, posteriorly, as the direct distance between the most lateral points of the toothed area on each half of the bone. The length of the dentigerous surface is the greatest distance of the toothed area measured directly from its posterior to its anterior points.

Neurocranial length (Nc.1) is measured directly, along the base of the skull, from the anterior point of the vomer to the posterior point on the condylar surface of the basioccipital.

Material

An asterisk indicates that skeletal preparations are available. Institutional abbreviations are, BMNH: British Museum (Nat.Hist.), RUSI: J.L.B. Smith Institute of Ichthyology, Grahamstown.

Tilapia guinasana (*ex.* Lake Guinas)

Lectotype: BMNH 1935.3.20:32

Paralectotypes: BMNH 1935.3.20: 33–51,* and 1935.3.20: 197–208

Other material from the original collection: BMNH 1935.3.20: 209–233* (see p. 24)

RUSI material collected by Ribbink *et al.*, 1988 and 1989

RUSI 35859 (large black)
 RUSI 35860 (large black)*
 RUSI 35861 (large olive)
 RUSI 35862 (large light blue)
 RUSI 35863 (olive)*
 RUSI 35864 (dark blue)*
 RUSI 35865 (light blue)*

RUSI 35866 laboratory reared; (Light blue; 60 mm S.L.)*
 RUSI 35867 laboratory reared; (Olive; 65 mm S.L.)*
 RUSI 35868 laboratory reared; (White and blue; 45 mm S.L.)*
 RUSI 35869 laboratory reared; (Olive, 50 mm S.L.)*
 RUSI 35870 laboratory reared; (Olive,* and light blue)
 RUSI 35871 laboratory reared; (white and blue,* and light blue)

RUSI material *ex* lake Otjikoto: RUSI 35485*

Tilapia species from southern Africa

T. sparrmanii: RUSI 30342 Okavango delta, Botswana*
 RUSI 24197 Okavango delta, Botswana*
 RUSI 19265 Lake Bangasi, St Lucia, Kwa-Zulu*
 RUSI 24223 Kwando river, Caprivi strip, Namibia*
 RUSI 2260 Limpopo system, Transvaal, RSA
 RUSI 27923 Mkuze, Yengweni Pan, Kwa-Zulu
 BMNH 1907.3.15: 44, Groot Olifants river, Transvaal, RSA.*

T. ruweti: RUSI 23616 Lake Ngami, Botswana
 RUSI 30343 Okavango delta, Botswana*
 RUSI 30126 Okavango delta, Botswana

T. rendalli: RUSI 23951 Okavango delta
 RUSI 26579 Nkomati river
 RUSI 27988 Sabi river, Skukuza, northern Transvaal, RSA*
 RUSI unregistered. Crocodile river, eastern Transvaal RSA*
 RUSI unregistered. Fish pond, J.L.B. Smith Institute (provenance unknown)*

RUSI unregistered. Okavango delta, Botswana*

Tilapia species from elsewhere in Africa:

T. brevimanus: BMNH 1912.4.1: 153*
T. buttikoferi: BMNH 1912.4.1: 163*
T. busumana: BMNH 1902.4.24: 41*
T. cabrae: BMNH 1911.6.1: 154*
T. guineensis: BMNH 1899.11.20: 4*
T. kottae: BMNH 1973.5.14: 1130–1133*
T. mariae: BMNH 1901.8.21: 38*
 BMNH 1985.11.12: 199–211*
T. tholloni: BMNH 1981.12.1: 1–12*
T. zillii: BMNH 1907.12.2: 3767*
 BMNH 1968.12.13: 30–42*

Oreochromis species:

O. alcalicus
alcalicus: BMNH 1966.12.9: 44–86*
O. a. grahami: BMNH 1982.4.22: 32–35*
O. amphimelas: BMNH 1967.8.17: 5–17*
O. mossambicus: RUSI unregistered alizarin preparations of laboratory raised juveniles

All radiographs used in this study are in the J.L.B. Smith Institute except that of *T. guinasana* lectotype, which is in the BMNH collection.

A REDESCRIPTION

Tilapia guinasana

Fig. 1

SYNONYMY. *Tilapia guinasana* Trewavas, 1936. *Novitates Zoologicae* 40: 72–73 (original description).

Tilapia (*Trewavasia*) *guinasana*; Thys van den Aude-naerde, 1968. *Documentation Zoologique, Musee Royal de l'Afrique Centrale* no. 14: xxvii–xxviii (definition of a new and monotypic subgenus, and designation of *T. guinasana* as type species).

No holotype was designated in the original description of

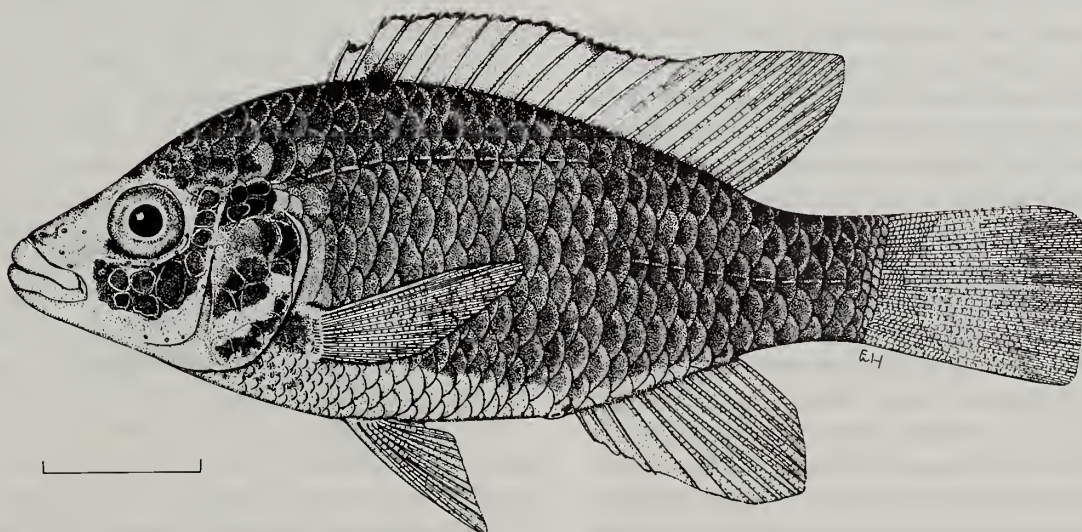


Fig. 1. *Tilapia guinasana*. Specimen from RUSI lot 35865; in life a light blue morph. Scale: 1 cm. Drawn by Elaine Heemstra.

the species. That description, according to Trewavas (1936) was based on 32 specimens, 60–137 mm total length, with specimens ‘. . . of less than 85 mm included for numerical characters only’; she did, however, note that smaller individuals have a relatively larger eye diameter and fewer teeth but ‘Otherwise they agree with older fishes’. The number of smaller fishes examined was not given.

A problem arose when I examined the supposed syntypical series in order to select a lectotype. The single jar housing these specimens contains 56 and not 32 specimens as indicated by Trewavas. The problem is further compounded by the museum register number (repeated on the bottle’s label) which covers only 20 specimens, namely 1935.3.20: 32–51.

It is impossible to identify, some 55 years later, the 32 specimens on which Trewavas based her description and thus to separate from the 56 specimens those which are truly syntypical and from which, legitimately, the lectotype may be selected. The largest specimen (137 mm total length) and the smallest (60 mm T.L.) studied by Trewavas are readily identifiable, but neither is in a good state of preservation and for that reason I would hesitate to select either as the lectotype. Fortunately another specimen (104.0 mm standard length, *ca.* 126 mm total length) has, under its operculum, a label in Dr Trewavas’ handwriting, bearing the legend ‘Holotype’. On the assumption that Trewavas examined this specimen and intended to designate it as the holotype, I have chosen it to be the lectotype and assigned to it the British Museum (Nat. Hist.) register number 1935.3.20:32.

That action does not resolve the problem of identifying the 31 other specimens (i.e. paralectotypes) on which the original description was based, except of course for the smallest and largest fishes. Since there is no guidance in the International Code of Zoological Nomenclature for settling this conundrum, I have selected, together with the largest and smallest specimens, 29 others to constitute the remainder of the type series. These now carry the BMNH register numbers 1935.3.20: 33–51, and 1935.3.20: 197–208 (the latter numbers still being available on the register page for 20th March 1935). My choice of these particular specimens was based on their relatively better state of preservation than that of the others, their representing as wide a range as possible of preserved colorations, and their coverage of the size range of specimens examined in detail by Trewavas.

Presumably the remaining 24 specimens can no longer be considered part of the type series; they now bear the BMNH register numbers 1935.3.20: 209–233.

The lectotype is a fish of indeterminable sex, 104.0 mm standard length and *ca.* 126 mm total length (the caudal fin margin is damaged), collected by Dr Karl Jordan from Lake Guinas, Namibia. Its preserved coloration, in ethyl alcohol (presumably after formalin fixation) is dark brown, slightly lighter ventrally, with darker brown centres to the flank scales.

In the absence of a phylogenetically based revision of the genus *Tilapia* (*sensu* Trewavas, 1983), it is difficult to comment on Thys’ proposed subgeneric categorization of *T. guinasana*. Thys defines the subgenus (within his definition of *Tilapia* which is more inclusive than Trewavas’) on the basis of it having 12 (rather than 16) scale rows around the caudal peduncle, and on its strongly granulate scales. Thys places *Trewavasia* between the nominate subgenus (comprising *Tilapia sparrmanii* and *T. ruweti*) and the other two subgenera of his ‘Section one’ subdivision of the taxon (Thys, 1968: xxvii–xxiv). On the grounds of its polychromatism (a feature

not known to Thys), *T. guinasana* certainly would seem to be a distinct lineage within the non-mouthbrooding tilapiines. Its larger and strongly granulate (i.e. rugose) scales may, however, be an ecophenotypic response to the water chemistry of the lake (see p. 35).

DESCRIPTION. The meristic and morphometric data used in this redescription of *T. guinasana* are derived mainly from the lectotype and twenty-one other specimens 49.0–151.0 mm standard length (the majority, 15 specimens, being in the size range 50–80 mm S.L.) collected by the Ribbink team in September 1989 (RUSI: 35859–35865). These fishes, rather than the paralectotypes, were used for morphometric and meristic studies because all are in a far better state of preservation, their live coloration is known, and they cover a wider size-range than does the type series. Information on tooth morphology and dental patterns (both oral and pharyngeal) and that on cheek squamation was supplemented by counts and observations made on the paralectotypes.

Trewavas’ (1936) morphometric ratios, and her meristic counts, do not depart from those obtained from the new material, and an examination of dental features (oral and pharyngeal) shows few differences between the two samples, except, to a small degree, in some features of the larger specimens now available. Unfortunately it is impossible to associate accurately the preserved colours of the type series with what is now known of coloration in living fishes and in the recently collected specimens which were segregated on the basis of their live colours before fixation. However, no outstanding differences were observed in the preserved colours shown by the two samples collected some 54 years apart.

The small sample of ‘large blacks’ and large specimens of light blue and olive fishes (totalling 4 specimens) is treated together with the others since in all but two morphometric features (eye diameter and cheek depth) they fall within the ranges determined for the smaller specimens. These proportional differences are explicable on the basis of allometric growth, but the figures for the two characters in the large specimens are given separately (in square brackets) and are not included in the means given for those features in the smaller specimens.

Regrettably from the taxonomic view point, but understandably and commendably from that of conservation, there are restrictions on the number of specimens which may be removed from Lake Guinas, hence the relatively small sample on which this redescription is based.

Depth of body 36.0–46.4 (mean, *M*, 40.8)% of standard length, with a slight tendency for large fishes to be the deepest; head length 30.8–37.1 (*M* = 33.4)%. Dorsal head profile in fishes <130 mm S.L. straight (sometimes with a slight concavity above the orbit) from a point above or almost above a vertical through the posterior margin of the preoperculum, and sloping at an angle of 40°–45° to the horizontal. This slope increases to about 50° in the four large fishes (139–151 mm S.L.), where the dorsal head-profile is more concave than in smaller individuals, a consequence of the anteroventral tip of the snout becoming slightly upturned.

Preorbital depth 15.5–23.1 (*M* = 20.1)% of head length; least interorbital width 29.7–36.4 (*M* = 34.8)%. Snout slightly broader than long (1.1–1.2 times), rarely as long as broad; its length 31.0–39.1 (*M* = 35.3)% of head length.

Eye diameter showing slight negative allometry with standard length, 25.4–32.4 (*M* = 28.7)% of head [20.4–25.5,

M = 22.3% in the four largest fishes]. Cheek depth showing positive allometry with standard length, 16.2–23.9 (M = 19.9)% of head length [24.5–28.3, M = 25.8% in the four largest fishes].

Lower jaw 33.3–39.1 (M = 35.2)% of head length, and from as long as it is broad to 1.3 times longer than broad (modal range 1.1–1.2 times longer). Mouth sloping slightly upwards; lips moderately thickened. Maxilla with a variable posterior extent, closely approaching a vertical through the anterior orbital margin in one specimen, but in the others reaching either a point midway between the nostril and the orbit or slightly beyond that point.

Caudal peduncle length 13.0–17.2 (M = 15.2)% of standard length, its length-depth relationships variable, the majority of specimens with the peduncle deeper than it is long (its length 80–90% of its depth) the others with the peduncle slightly longer than deep (1.1–1.2 times). No correlation was found between this ratio and specimen size or coloration.

GILL-RAKERS. 8–11 (rare), mode 10, in the outer row on the ceratobranchial of the first arch. The rakers are short and stout (the anterior one or two shorter than the succeeding ones) and have a characteristic pyramidal shape (Fig. 2) quite unlike the narrow-based, flattened, triangular and more elongate rakers in *T. sparrmanii*. Microbranchiospines are present on the outer faces of gill-arches 2 to 4.

SCALES. On all parts of the body the scales are cycloid and have a very characteristic rugose appearance over their entire exposed surfaces, but especially over the central region in scales on the cheeks and flanks. When compared with the scales of *T. sparrmanii*, those of *T. guinasana* are thicker and denser.

There are 25(f5), 26(f12), 27(f4) or 28(f1), mode 26, scales in the lateral series. In one specimen no scales in the upper lateral-line are pored, but in the others 11(f1), 12(f2), 13(f3), 14(f4), 15(f5), 16(f5) or 17(f1) pored scales are present; pored scales in the lower lateral-line number 7(f2), 8(f7), 9(f7), 10(f5), or 11(f1).

The lowest row of cheek scales is often deeply embedded in a thick layer of skin and thus is invisible unless the skin is removed. This 'hidden' row probably accounts for the greater incidence of two scale rows in the new material than apparently was the case in the specimens examined by Trewavas (1936). Without dissection, many more fishes would appear

to have only a single row, (as indeed some do) and thus the difference in the number of cheek scale rows between *Tilapia sparrmanii* and *T. guinasana* noted by Trewavas is artificially exaggerated. Whenever a lower row is present, its scales are much smaller than those in the upper row and are thinner and less rugose.

The frequency of cheek scale rows for the 'type' material, at least part of which Trewavas examined, is: 1 row (f3), 2 rows (f45), plus 6 specimens with a single row on one side and two on the other. For the new material, the frequencies for the different conditions are, respectively, 2, 15 and 4. Thus, for the two samples, the modal condition is 2 rows, with a single row occurring less frequently than the laterally asymmetrical situation of a single and a double row.

There are 12 scales (13 in one fish) around the caudal peduncle.

The slight size transition between the scales on the chest and those ventrolaterally on the flanks and belly is a gradual one. Except apically, the median scales on the chest are as large as those immediately lateral to them; the apical scales are noticeably smaller.

FINS. The dorsal has a total of 22(f1), 23(f10) or 24(f10) rays (21 specimens only are included here as one fish has an irregular, overlapping junction between the spinous and soft parts of the fin, suggesting some teratological condition), comprising 11(f1), 12(f6), 13(f12) or 14(f2) spinous and 10(f6) or 11 (f15) branched elements. The anal fin has three spines and 7(f1), 8(f4), 9(f13) or 10(f4) rays.

The tips of the longest pectoral rays reach or almost reach a vertical through the anus; the pectoral fin length ranges from 25.3–29.2 (M = 26.8)% of standard length and 74.5–87.5 (M = 80.0)% of head length, neither ratio showing any allometric relationship with standard length.

The longest ray of the pelvic fin extends posteriorly to a little before the anus or to a position between that point and the first anal fin spine. Apparently there is no correlation between the relative length of this fin and the fish's sex or state of sexual activity.

Posteriorly, the margin of the caudal fin varies from truncate to almost rounded, but is truncate or subtruncate in the majority of specimens. The fin is scaled proximally in a roughly crescentic pattern, the horns of the crescent extending to a point about one quarter to one third of the way along the fin's upper and lower margins.

ORAL TEETH. In both jaws most outer teeth are bicuspid. Some unicuspid occur posteriorly, their number on the premaxilla ranging from two or three to as many as fourteen; in the dentary usually only about six such teeth are present. There is no obvious correlation between the number of premaxillary unicuspid and the fish's size, although the lower counts were found in smaller individuals.

Bicuspid teeth (Fig. 3) have a slender body (about half the height of the tooth) which gradually expands into a broader, flattened, and very unequally bicuspid crown. The minor cusp is somewhat obliquely pointed, the major one obliquely truncated and a little protracted, a crown form commonly found amongst *Tilapia* species.

Like the bicuspid, the unicuspid have a relatively compressed crown, but one which is not noticeably wider than the cylindrical body; the tip, at least in unworn teeth, is acutely pointed.

Both bi- and unicuspid teeth are curved adorally from a

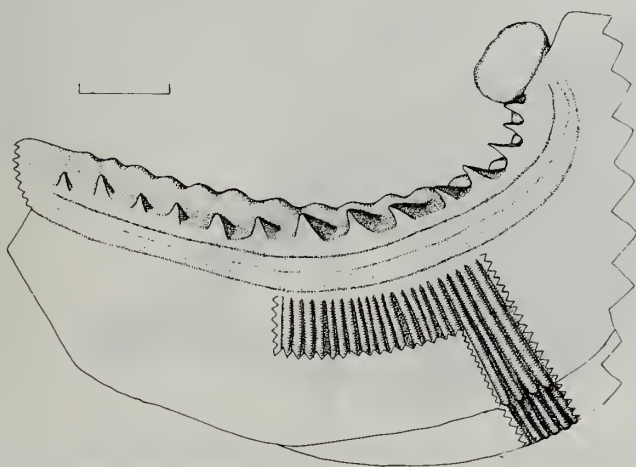


Fig. 2. *Tilapia guinasana*. Outer row gill-rakers on the first gill-arch. Specimen from RUSI lot 35865. Drawn by Elaine Heemstra.



Fig. 3. *Tilapia guinasana*. Oral dentition in part (see also Fig. 9). Anterior and anterolateral region of the right dentary, viewed obliquely from above. The bullate ventrolateral region of the dentary (see p. 30) is clearly visible. Specimen RUSI 35865 (dark blue), 76.0 mm S.L. Magnification $\times 26$.

point about midway along their height. Bicuspid teeth situated anteriorly on the dentary have the most pronounced curvature, in that way ensuring, because of their low implantation on the jaw, that the crowns are almost vertically aligned when the mouth is closed.

Posteriorly, the outer row of teeth on each side of the dentary has a distinct mediad inclination from a point almost opposite the termination of the inner tooth row (Fig. 9, p. 31). As a result, the dental arcade has an approximately horse-shoe shaped outline in occlusal view (a feature not shared with *T. sparrmanii* or *T. ruweti*).

Some growth related dental changes are apparent in the sample studied. The larger specimens usually have very weakly bicuspid teeth (almost shouldered unicuspid) intercalated amongst the true bicuspid teeth, and a few unicuspid teeth occur anteriorly and anterolaterally in both jaws. It is impossible to ascertain whether the shouldered teeth are the result of wear, or are elements in an ontogenetic series; the presence of true unicuspid teeth, however, seems to be explicable on the latter basis.

Inner-row teeth in fishes of all sizes are tricuspid, generally with the cusps of equal size and length, but some do have the centre cusp taller and broader than those flanking it.

Anteriorly, and to a slight extent anterolaterally, the inner teeth are arranged in several series, narrowing to a single row which never extends along the entire length of the outer row.

In fishes 40.0–151.0 mm standard length there are 40–70 (modal range 46–50) outer premaxillary teeth, the number showing no clear-cut correlation with the individual's size, although the highest number occurs in the largest specimen examined. The number of inner rows, however, does show some positive correlation with size; the largest specimens (140.0 and 151.0 mm S.L.) have, respectively, six and five rows in the upper jaw and six and four in the lower jaw. Smaller fishes ($n = 20$) have 3(f4), 4(f10) and 5(f6) rows in the upper jaw, and 3(f9), 4(f8) and 5(f3) in the dentary.

PHARYNGEAL JAWS AND DENTITION. When *in situ*, the upper pharyngeal bones have the typical tilapiine cardiform outline (see Greenwood, 1987, fig. 4).

The lower pharyngeal bone has a short keel, its length

contained 2.5–3.0 times in the length of the dentigerous area, the latter being as broad as it is long or slightly broader than long. When viewed ventrally, much of the body of the bone underlying the dentigerous surface has an inflated appearance (Fig. 4).

The lower pharyngeal teeth are closely and regularly arranged, especially over the posterior third of the dentigerous area. Most teeth are of the typical tilapiine 'kukri' form (Greenwood, 1987: 196–7; fig. 30), with the depth of the 'blade' reduced in teeth on the posterior quarter of the bone. Only those teeth in the posterior three or four transverse rows are bicuspid, but the minor cusp is small and in the form of a short, compressed ridge at the base of the major cusp. The latter is tall, with a weak, anteriorly directed curvature.

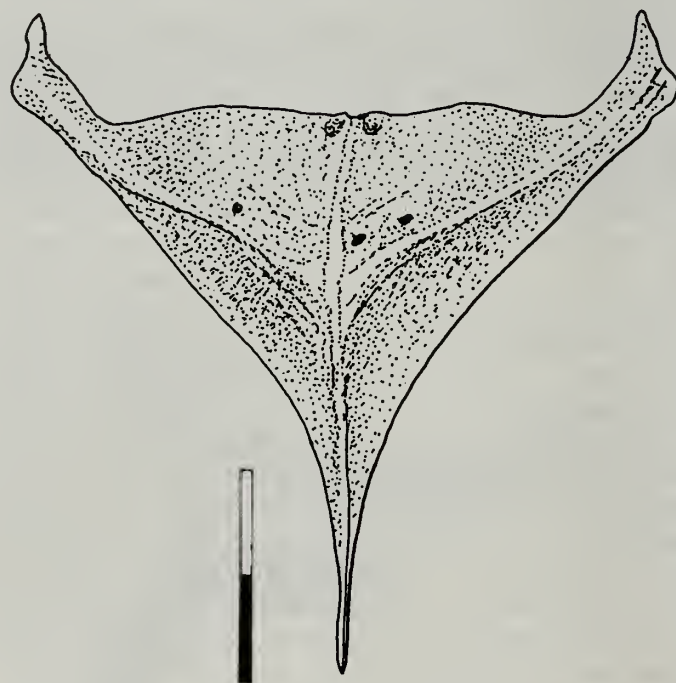


Fig. 4. *Tilapia guinasana*. Ventral aspect of the lower pharyngeal bone. Specimen from the paralectotypical series, BMNH 1935.3.20: 33–51; 70.0 mm S.L. (colour in life unknown, but probably light blue). Scale = 2 mm. Drawn by Gordon Howes.

In their overall morphology, the pharyngeal jaws and dentition of *T. guinasana* are typical for the species comprising Section I of 'Thys' (1968) tilapiine classification.

NEUROCRANIUM. Data on the neurocranium were derived mainly from five wild-caught specimens representing the colour morphs 'light blue' (2 specimens), 'olive', 'dark blue' and 'large black', covering the size range 45.0–135.0 mm S.L. (neurocranial lengths 12.0–31.5 mm). Additional information, used in the Discussion (p. 35), was obtained from a number of smaller, laboratory-raised fishes.

Osteologically, the neurocranium (Figs 5–8) is probably the most outstanding feature of *T. guinasana*, both when compared with the neurocranium of comparable sized specimens of other *Tilapia* species (*sensu* Trewavas, 1983), and with the skull in *Oreochromis* and *Sarotherodon* species as well (see also Discussion, p. 35). No skeletal material of *Danakilia* was available for comparison.

In particular, *T. guinasana* differs, apparently uniquely, in the appearance of its dorsicranium (Figs 5–8). This is especially noteworthy for the thickness of the frontals, the cambered surface of the supra- and interorbital regions of those bones, the convex rather than concave surfaces of the parietal and supraoccipital between the base of the supraoccipital crest and the fronto-parietal crest, and in the convex surface of the parietal between its contribution to the fronto-parietal crest and the bone's suture with the pterotic. The general appearance of these skull regions in *T. guinasana* is thus

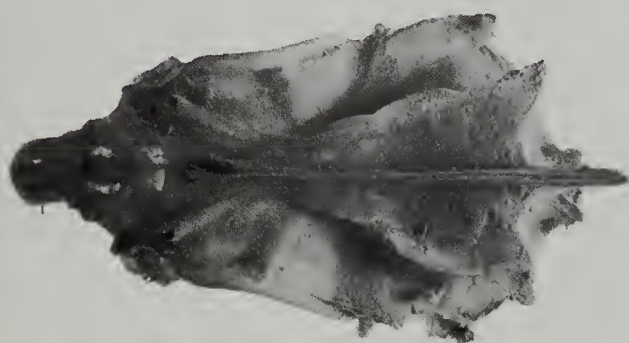
one of moderate inflation and roundness, especially when compared with the skull roof in *T. sparrmanii* of a similar size.

Superficially, the greater part of each frontal's dorsal surface (except for the low median crest and the bone's narrow supraorbital margin) has an inflated appearance and, when the skull is viewed from in front, a noticeable, medio-laterally directed camber; in other *Tilapia* species this area is either flat or slightly concave. The camber is most marked in the smallest skull (12.0 mm neurocranial length) and least obvious in the largest one (31.5 mm Ncl.). This region of each frontal is distinctly ornamented with short, low, often curved, confluent and somewhat randomly orientated ridges as well as with horizontally directed, cave-like pits (Figs 6–8). Such ornamentation was not seen in any other tilapiine skull examined.

When illuminated from below, the frontal gives the appearance of having trapped in it a large number of air or oil bubbles, and when sectioned it has a rigid but sponge-like texture between its inner and outer faces of compact bone (Fig. 8). This hyperdevelopment of spongy bone is partly responsible for the frontal's inflated appearance, and entirely responsible for its relative thickness. Similar spongy bone occurs in the epiotic.

The cambered, convex curvature of the frontal's upper surface is apparent, sometimes to an even more marked degree in other tilapiines, but, however, only when skulls

A



B

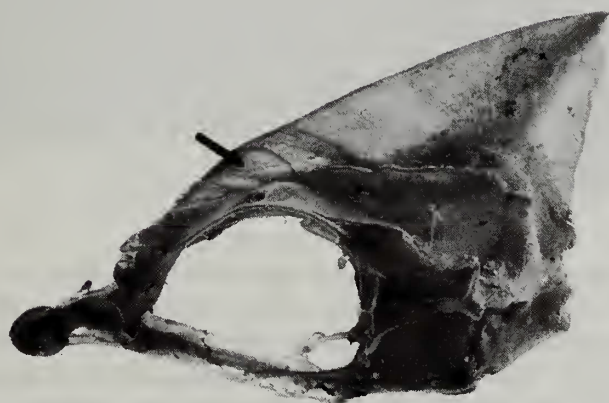
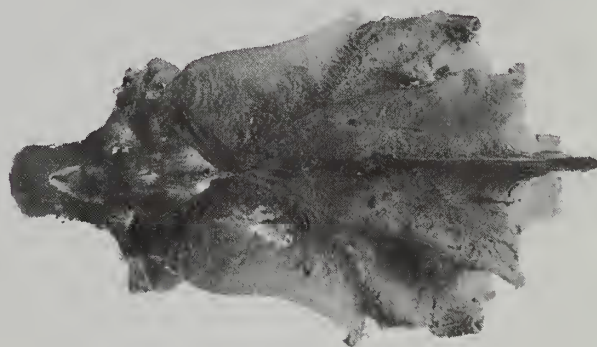


Fig. 5. A. *Tilapia sparrmanii*. Neurocranium in dorsal and in left lateral views. The prominent median frontal crest is arrowed. Specimen from RUSI lot 24197 (Okavango delta), 82.0 mm S.L., neurocranial length 20.0 mm. Magnification $\times 3$.

B. *Tilapia guinasana*. Neurocranium in dorsal and in left lateral views. The low median frontal crest (arrowed) is barely visible above the frontal's dorsal surface; the basisphenoid was lost during preparation of the skeleton. Specimen from RUSI lot 35864 (dark blue), 78.0 mm S.L., 18.0 mm neurocranial length. Magnification $\times 3.2$.

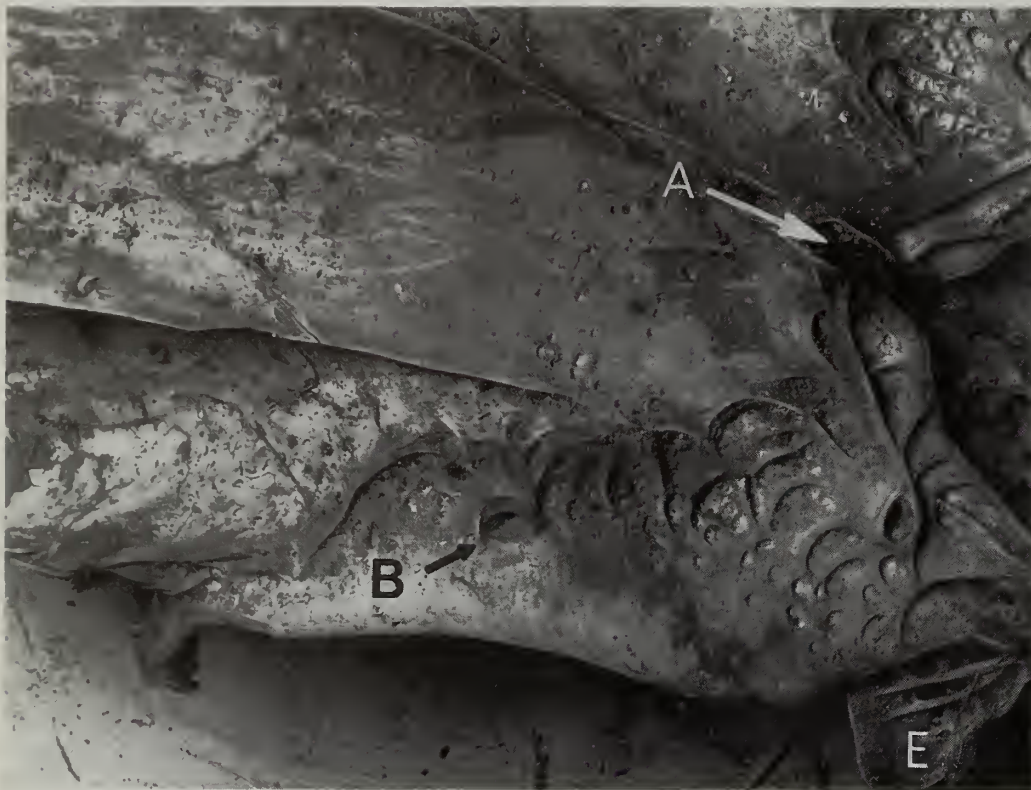
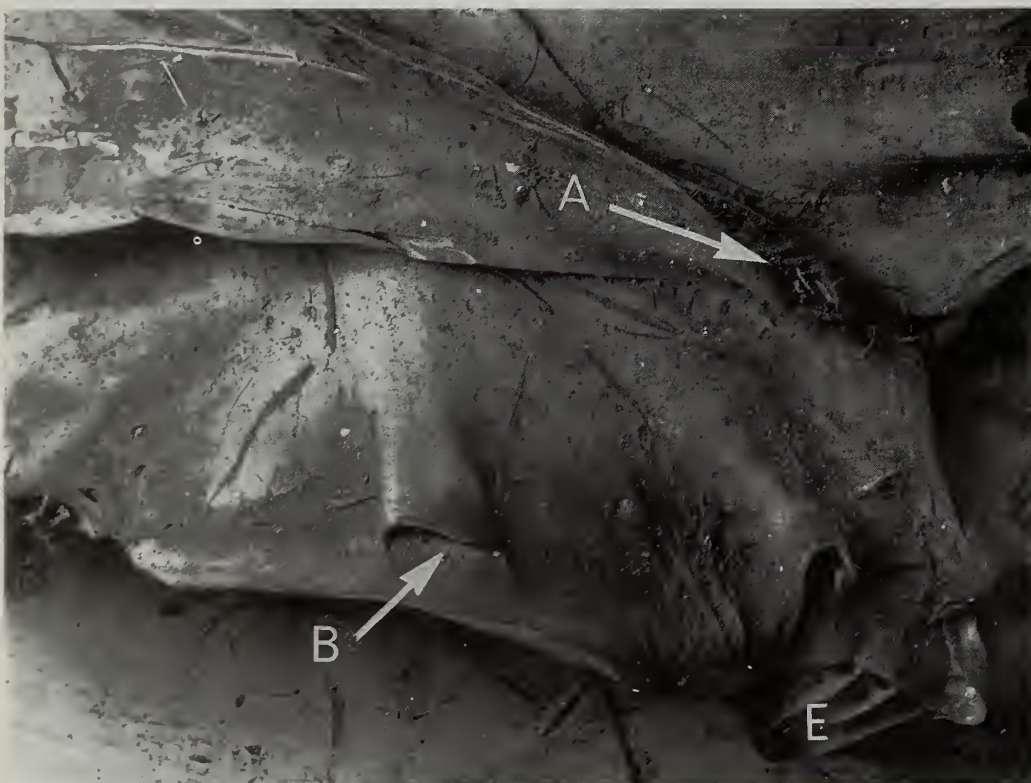
**A****B**

Fig. 6. A. *Tilapia guinasana*. Dorsal view of right frontal (greater part) and a small area of the left frontal showing ornamentation of the bones. Specimen orientated with the midline at 30° to horizontal, anterior is to the right. Arrow A indicates the coronary pore of the cephalic lateral-line system, and arrow B the right supraorbital pore of that system; E: right lateral ethmoid. specimen from RUSI lot 35865 (light blue), 76.0 mm S.L., 18.0 mm neurocranial length. Magnification × 8.

B. *Tilapia sparrmanii*. Comparable area of the dorsicranium. Arrows and abbreviation as in Fig. 6A. specimen as in Fig. 5A. Magnification × 8.

smaller than those of the wild-caught *T. guinasana* specimens are examined. (It is also more marked in the smaller, laboratory-raised *T. guinasana* studied, see p. 35). Unlike *T. guinasana*, none of the other tilapiine species examined shows the spongy hyperosteosis characterizing the frontal and epiotic in that species. The 'rounded' appearance, found only in the juveniles of the other tilapiines, is thus attributable entirely to the shape, at that stage of their ontogeny, of the bones involved. Questions raised by frontal hyperosteosis and the curvature of the bone's dorsal contours in adult *T.*

guinasana are discussed in detail later (p. 35).

The orbital face of the frontal is smooth and the bone compact. When viewed laterally there is no marked invasion of the orbit by the ventral surface (Figs 5A & B) of that bone. In other words, the 'inflation' of the frontal is directed dorsally.

Apparently as a consequence of this inflation, the cephalic lateral-line tubules, except for their pores, are not readily visible as intrusions onto the frontal's surface, as they are in other *Tilapia* species except *T. ruweti* (which does not,



Fig. 7. *Tilapia guinasana*. Rugose ornamentation on the right frontal in the area between the origin of the frontal's contribution to the frontoparietal crest and the supraorbital opening of the cephalic lateral-line system. Specimen as in Fig. 5B. Magnification $\times 36$.



Fig. 8. *Tilapia guinasana*. Posteromedian area of the frontals to show their ornamentation. The ridge situated over and partly anterior to the laterosensory canal opening into the infraorbital canal (see this page) is clearly visible on the left frontal.

Immediately anterior to this ridge, part of the compact superficial layer of bone has been removed to reveal the spongy bone (arrow A) intercalated between the upper and lower layers of compact bone.

Skull orientated so that the vomer points to twelve o'clock. Specimen as in Fig. 5B. Magnification $\times 12$.

however, show any inflation of its frontals).

Except in the largest skull there is little development of the median frontal crest formed along the suture line between the left and right bones and which continues forward the anterodorsal outline of the supraoccipital crest. Even in the largest *T. guinasana* skull the crest is relatively lower than that in comparable-sized neurocrania of other *Tilapia* species, especially *T. sparrmanii* (Fig. 5). A reduction of the crest's height in small specimens, relative to that in larger ones, is, however, a feature of all the small *T. sparrmanii* skulls examined (the only species for which an adequate growth series was available).

Another unusual and probably unique feature of the frontal in *T. guinasana* is the development of an obvious, sometimes prominent, and slightly curved ridge running on or a little anterior to the passage through that bone of the lateral-line tubule opening into the infraorbital canal series (Fig. 8). The ridge originates on the frontal below and contiguous with the frontal portion of the fronto-parietal crest slightly anterior to its suture with the parietal portion. It runs parallel to, and in contact with the crest for a short distance, then curves sharply laterad and downwards towards the opening of the tubule. The ridge is best developed in the larger skulls.

The fronto-parietal crests are relatively low and are of variable anterior extent. In four skulls (12.0–19.0 mm Nc.l.) the crests extend to the level of the supraorbital pore of the frontal lateral-line tubule; over their entire length the crests incline a little towards the midline (and one another) but do not meet medially. The fifth, and largest skull (31.5 mm Nc.l.), has more prominent crests that are more medially inclined and contact the median frontal crest a little posterior to the coronary lateral-line pore.

In the absence of much information about variability in fronto-parietal crest prominence, and their anterior extension and alignment in *Tilapia* species, little importance can be attached to the situation in *T. guinasana*. However, personal observations show that in this species and *T. sparrmanii* all three conditions are similar, but in *Tilapia ruweti* from the Okavango system the crests are lower than those in *T. guinasana* and converge anteriorly but do not meet the median frontal crest.

The supraoccipital crest is variable in its outline, and differs little from that in *T. sparrmanii*. Its height, expressed as a percentage of neurocranial length, ranges from 27.5 to 34.6%. When viewed laterally, however, the crest appears to be less expansive and shorter than in *T. sparrmanii*. This impression is a consequence of the low and short median frontal crest in *T. guinasana*. The longer and more prominent crest in *T. sparrmanii* continues forward the dorsal outline of the supraoccipital crest, thus seeming to increase both the latter's area and its anterior extent. A similar apparent shortening of the crest occurs in *T. ruweti*, and for the same reasons as in *T. guinasana*.

In an early paper considering intragroup relationships of the then single genus *Tilapia*, Trewavas (1973: 20–23) paid considerable attention to the spatial relationships of the mesethmoid (supraethmoid) and vomer. From her study, Trewavas concluded that the majority of species referable to her revised *Tilapia* concept (*op. cit.*: 20) had the supraethmoid contacting the vomer, with, in a very few exceptional cases the contact being confined to one side only. In contrast, relatively few (*viz.* 5) *Tilapia* species, and all the *Sarotherodon* species she examined, had the vomer free from the supraethmoid. Two of the five *Tilapia* species in this group, however, had a unilateral contact between the bones.

Trewavas (*op. cit.*) put forward a possible functional explanation for this dichotomy in supraethmoid-vomer relationships. Namely, that the separation of the bones was a consequence of the broader head in *Sarotherodon* species, a proportional change that evolved in association with predominantly microphagous feeding habits and, concomitantly, a reduction in the stresses and strains on that region of the skull in these fishes as compared with the situation in, for example, a piscivore. No explanation, however, was given for the exceptional *Tilapia* species (see above). In a later discussion, Trewavas (1983), cited several exceptions to that supposed correlation, and pointed out a number of cases amongst the Cichlidae where the existence of a supraethmoid free from the vomer must be considered as evolutionary convergences.

A study of the vomer-supraethmoid condition in specimens of *T. guinasana*, and a number of other *Tilapia* species, leads me to suggest that the nature of the bones' relationships could have an ontogenetic basis and thus be correlated with the size of the specimen in relation to the maximum size reached by individuals of a particular species.

In wild-caught *T. guinasana* examined, there is no contact between the bones in three specimens (45.0, 76.0 and

78.0 mm S.L.), slight contact in a fourth (73.0 mm S.L.) and substantial contact in the largest fish, 135.0 mm S.L. There is no contact in the four laboratory-raised specimens of 44.5 to 65.0 mm S.L. Likewise, no contact occurs in four *T. sparrmanii* 41.0–65.0 mm S.L., partial and unilateral contact in one of 80.0 mm S.L., and bilateral contact in a fish of 92.0 mm S.L. All these were wild-caught fishes and each came from a different locality. Trewavas (1973: 22) records that the bones are in contact in this species, but gives no sizes for the three specimens she examined.

A similar size-related correlation exists in *T. rendalli*, a species which Trewavas (*op. cit.*) lists, again without length data, as having the vomer and supraethmoid in contact. In the 40.0, 80.0 and 87.0 mm S.L. specimens I examined the bones are free from one another, but in a specimen of 215.0 mm S.L. there is contact like that in the 200.0 mm fish illustrated by Trewavas (1973: fig. 13).

The largest of the *T. ruweti* I examined (65 mm S.L.) has the bones separated.

That, in tilapiine fishes the relationships of the two bones may not always be correlated with absolute size is, however, suggested by a lack of contact in individuals of several *Sarotherodon* species (some now included in the genus *Oreochromis*; see Trewavas 1983) of a size larger than individuals of those *Tilapia* species in which the bones are in articulation, as for example in the *Oreochromis shiranus* examined and figured by Trewavas (1973: fig 14A). In these exceptional taxa it would seem that either the juvenile condition is retained in fully adult and large fishes, or the onset of articulation is delayed until a growth point nearer the modal maximum length for the species is reached. Further research is needed before a clearer understanding of the phenomenon is obtained and its phylogenetic significance, if any, can be determined (for comments on the latter issue, see Trewavas, 1973 and 1983).

Apart from its characteristic dorsicranial morphology, the skull of *T. guinasana* shows no outstanding or unique features. Its overall proportions are of the generalized *Tilapia* type, as are its articulatory apophysis for the upper pharyngeal bones, and the well-ossified lateral commissure of the *pars jugularis* (Greenwood, 1986).

JAWS. There are no species-specific characteristics associated with the upper jaw bones. The dentary, however, does depart somewhat from the usual *Tilapia* condition (Fig. 9). Before curving medially, the lateral aspects of this bone, at a point slightly below its dentigerous surface, have a distinct outward bulge, as does that region of the bone forming the lower limb of the indentation which receives the anguloarticular. As a result of this curvature, the lower part of the dentary has a rather bullate appearance, especially when compared with its counterpart in *T. sparrmanii*. In *T. guinasana*, the dentary's ventral profile also slopes more steeply upwards than in *T. sparrmanii*, a difference which seems to enhance the bullate appearance of the entire bone in *T. guinasana*.

When compared with the dentary in some but not all specimens of *T. sparrmanii*, the bone in four of the five *T. guinasana* examined has a relatively greater mediad expansion of its dentigerous surface anteriorly and anterolaterally. In these specimens, this expanded, ventrally sloping and cliff-like area also has a rather inflated appearance. Both features are less marked in the fifth skeleton, prepared from a 'large black' individual, 135.0 mm standard length.

The exceptional *T. sparrmanii* specimens also show an



Fig. 9. *Tilapia guinasana*. Lower jaw in occlusal view to show the 'horseshoe'-shaped dental arcade, the unicuspid teeth situated posteriorly in the outer tooth row of the dentary, and the anterior, lingually directed, cliff-like expansion of that bone. Specimen from RUSI lot 35865 (dark blue), 76.0 mm S.L. Magnification $\times 10$.

expanded area like that in the smaller *T. guinasana*, but it does not have the same inflated appearance in this species. Judging from the *Tilapia* material studied, a marked and distinct expansion of this region of the dentary is not a common feature; it is not developed in either *T. ruweti* or *T. rendalli*, the two taxa for which material was available covering, *in toto*, the same size-range as the *T. guinasana* examined.

In the *T. guinasana* and *T. sparrmanii* examined the size of the expanded area is correlated with the number of inner tooth rows present, being widest in specimens, of both species, with the highest (and numerically comparable) number of rows.

INFRAORBITAL BONE SERIES. The series is complete (that is, six elements including the lachrymal and dermosphenotic) in all but one of the five *T. guinasana* skeletal preparations. In the exceptional fish there are only five elements on one side, apparently as a result of fusion between the third and fourth bones. This specimen is also exceptional in having four (not five) openings to the lateral-line system in both lachrymal bones; all other specimens, including the type-series and the specimens used in this paper, have the usual number of five.

VERTEBRAL COLUMN. There is a total, including the urosty-

lar centrum, of 25(f2), 26(f17) or 27(f2) centra in the specimens radiographed (including the holotype), comprising 12(f14) or 13(f7) abdominal and 12(f1), 13(f6), 14(f13) or 15(f1) caudal elements. Where it could be identified on the radiographs, the spondylophysial process is on the third vertebra. A single supraneural (predorsal) bone is present.

CAUDAL FIN SKELETON. Judging from the 20 radiographs in which the caudal fin skeleton is clearly visible, there is a marked tendency for its upper elements, including the epurals, either to be fused, partially fused or closely apposed to one another. In nine specimens the 3rd and 4th hypurals are fused into a single plate, and in ten others these bones are either partially fused or in very close apposition. In eight fishes only a single epural is visible. From its size, it would seem to represent a fusion of the usual two bones.

There is no suggestion that fusion of either the hypurals or the epurals is more, or most, frequent in any one particular colour morph, and in no specimen are the two lower hypurals closely apposed to one another.

Little published information is available on the caudal osteology of tilapiine fishes (Vandewalle, 1973; Trewavas, 1983). Based on that information and on personal observations, it seems that fusion of the epurals, or their reduction to a single element in some other way, has not been recorded previously. Hypural fusions, in various combinations have, however, been recorded.

OTHER OSTEOLOGICAL FEATURES. The palatoquadrate arch, the suspensorium, opercular series, hyal bones and the branchial skeleton in *T. guinasana* do not depart in any outstanding way from the supposed generalized condition seen, for example, in *Tilapia sparrmanii*. However, the dorso-posterior margin of the suboperculum in *T. guinasana*, unlike that in *T. sparrmanii*, slopes forwards (it is vertical in *T. sparrmanii*); as a result, there is a distinct excavation in the posterior margin of the opercular flap at the point where the operculum and suboperculum are in articulation (see also p. 33).

COLORATION. Detailed descriptions of the live colours in the five principal and four subsidiary morphs (p. 22) are given by Ribbink *et al.*, (1991).

Preserved coloration is extremely varied. The dark blue and olive morphs (p. 22) range from uniformly light- to dark-charcoal and black. One specimen (dark blue in life) is a blotched grey-brown overlying a yellowish ground colour on the flanks, almost uniformly dark charcoal on the dorsal surfaces of the head and body, and yellow with a few dark blotches on the ventral and ventrolateral aspects of the head, chest and anterior part of the belly. Traces of spaced vertical bars are faintly visible on the flanks and caudal peduncle of lighter coloured individuals, and all fins are dusky or black.

Preserved light-blue morphs are a less intense version of the blotched dark blue fish described above, with the yellow colour extending further over the head and along the belly to about the level of the anus. In lighter individuals, the dark pigment on the flanks appears to be concentrated into spots at the scale centres, the area around the spots being much lighter and greyish in colour. All fins, including the pelvics, are greyish-yellow.

The enigmatic 'large' fishes (see p. 22) are represented in the collection by two colour forms. Three specimens, including the fish identified as olive when alive, are uniformly and intensely black on the head and body; the fins, including the

pectorals and pelvics are black basally but shade to charcoal-grey distally. The other large fish, classified when alive as 'Light blue', is coarsely blotched, black on yellow, with yellow lips and lower jaw, and all fins, except the pectorals and pelvics dark over most of their length but lightening to yellow near their tips. The pectorals are black basally but otherwise greyish, the pelvics black except for their yellowish tips.

No 'Tilapia-mark' is visible on any of the preserved specimens, wild-caught or laboratory-raised, over 52.0 mm S.L. In one laboratory raised fish, 44.5 mm S.L., a definite mark was present, and in another, 50.0 mm long, the dorsal fin has three, small, comma-shaped and serially arranged dark spots in the region of the fin where a 'Tilapia'-mark should occur.

The loss of a 'Tilapia mark' at such a small size contrasts strongly with the situation in *T. sparrmanii* where, amongst the populations I examined, a fully developed mark is retained in sexually active fishes of much larger sizes (see also Jubb, 1967).

DIAGNOSIS

In the original diagnosis for *T. guinasana*, Trewavas (1936) compared the species only with *T. sparrmanii*, the geographically nearest *Tilapia* species and also the one most closely resembling the new taxon. Since 1936 another species of the group (*sensu* Thys, 1968) to which both *T. guinasana* and *T. sparrmanii* belong, has been described, namely *T. ruweti* (Poll & Thys, 1965), and must be included in any diagnosis.

Tilapia guinasana is immediately distinguishable from both species on the basis of its polychromatism (a feature of which Trewavas was unaware) and the fact that none of its colour morphs resembles the adult coloration in either of the other two species. The juvenile coloration, especially of the body, does, however, approach that in some colour phases of *T. sparrmanii* adults (but not sexually active individuals) and juveniles. (Personal observations on aquarium specimens of both species, the *T. sparrmanii* being wild-caught individuals from the Okavango delta, and the *T. guinasana* wild-caught fry subsequently raised in aquaria at the J.L.B. Smith Institute).

Although superficially *T. guinasana* and *T. sparrmanii* are similar in gross appearance, the former has an obviously more linear and less decurved dorsal head profile, and the upward slope of its lower jaw is less marked.

Trewavas (1936) lists a number of morphometric features separating the two species, but current knowledge of intraspecific variability indicates that none can be considered as critically diagnostic. Nevertheless, although there is an interspecific overlap in ranges for body depth and length of lower jaw (Thys, 1964; personal observations on South African and Okavango specimens), the mean body depth in *T. sparrmanii* is greater than that in *T. guinasana* (42.6–52.1, $M = 45.8\%$ of S.L., cf. 36.4–46.6, $M = 40.0\%$ for the species respectively), and the mean lower jaw length is greater in *T. guinasana* than in *T. sparrmanii* (33.3–39.1, $M = 35.2\%$ head length, cf. 28.4–33.3, $M = 31.2\%$).

Oosthuizen *et al.*, (1991) note that the most outstanding morphometric difference between the species is in the ratio of head width to standard length (35.3% S.L. in *T. guinasana*, 15.9% S.L. in *T. sparrmanii*). Regrettably, the authors neither

state how head width was measured, nor give the size of the samples measured, and neither is a list of study material provided. Assuming their measurement is the usual one, then the figure for *T. guinasana* can only be a *lapsus* or a typographical error. On the basis of my material there is little difference between the species in the ratio head width/standard length (modal figures 17.0% S.L. and 17.5% S.L. for *T. guinasana* and *T. sparrmanii* respectively). That point apart, I would agree with Oosthuizen *et al.*'s conclusion that differences in other morphometric characters are insufficient to separate the two species, and that differences in their meristic features are also inadequate for that purpose, the more so since environmental factors could influence the phenotypic expression of such features.

Body scales are generally larger in *T. guinasana* than in *T. sparrmanii* (lateral scale count 24–27, mode 26, cf. 26–29, mode 28; circumpeduncular count 12, rarely 13, cf. 16, rarely 14 or 15 in *T. sparrmanii*). The scales are markedly rugose in *T. guinasana*, but only slightly so in *T. sparrmanii*, and are thicker in *T. guinasana* (but see Discussion, p. 35). Trewavas (1936) indicates that there are usually fewer rows of cheek scales in *T. guinasana* than in *T. sparrmanii*, but she was misled (see p. 25) in her counts by the deeply embedded lowermost row in the former species (another feature distinguishing the two taxa).

There is an interspecific overlap in the total dorsal fin-ray counts for *T. guinasana* and *T. sparrmanii* but a slight difference in the modal number of rays (25 cf. 23 or 24 for the species respectively). Likewise there is an overlap in the number of spinous dorsal rays (13–15 in *T. sparrmanii* cf. 11–14 in *T. guinasana*) but the mode, 13, is lower in *T. guinasana*.

Another feature used in the original diagnosis, the supposed greater number of tooth rows in the upper jaw of *T. guinasana* (4–7 cf. 3 or 4, rarely 5 in *T. sparrmanii*) is no longer effective when fishes over a wide size-range are compared and when *T. sparrmanii* from populations other than those used by Trewavas (1936) are examined.

The short, near pyramidal gill-rakers (p. 25) are diagnostic for *T. guinasana*.

The nature of the pharyngeal dentition and the overall shape of the lower pharyngeal bone are very similar in both species, but the bone in *T. guinasana* is clearly more bullate ventrally than it is in *T. sparrmanii*.

Some of the various neurocranial features discussed on pages 27–30 would seem to be diagnostic for the species, at least over a certain size-range. Differences in the cambering of the frontals, and the superficial visibility of the lateral-line canals in that bone are, however, less diagnostic when skulls of *Tilapia guinasana* 45–78 mm S.L. are compared with those of *T. sparrmanii* specimens less than 40 mm S.L. Again, when the largest *T. guinasana* skull (from a fish 135.0 mm S.L.) is compared with skulls of *T. sparrmanii* specimens over 50 mm S.L., the differences are also less marked. Nevertheless, even in the latter comparison, the relevant areas of the frontals in *T. guinasana* have a somewhat more inflated appearance than do their counterparts in *T. sparrmanii*.

The very poorly developed median frontal crest (p. 28) of *T. guinasana* in the size range 45–78 mm S.L. is comparable with the condition found in the skull of a 41 mm S.L. *T. sparrmanii*, but not with the prominent crest in larger specimens of that species; even in the largest *T. guinasana* skull examined the crest is relatively lower and less prominent than in any *T. sparrmanii* skull from specimens over 40 mm S.L.

The possible significance of these size-related differences, and of the other departures from the *T. sparrmanii* condition in the skull of *T. guinasana*, are discussed in more detail later (p. 34).

Consistent differences in the skulls of the two species, irrespective of an individual's size, are the relatively inflated epiotic in *T. guinasana*, the hyperostosis and sponginess in parts of the frontal, (p. 27), the rugose and pitted surface of that bone, and the presence of a prominent ridge above or close to the cephalic lateral-line tubule opening into the infraorbital part of that system.

Throughout the size-range of skeletal material examined, the lateral aspects of the dentary and anguloarticular bones in *T. guinasana* are distinctly more bullate than those in *T. sparrmanii*. A buccally directed, cliff-like expansion of the inner aspect of the dentary is also developed in *T. sparrmanii*, but apparently only in specimens having higher numbers of inner tooth rows on that bone; it is, however, never as prominent as the mental thickening in *T. guinasana*. Unlike *T. guinasana*, the dental arcade of the dentary in *T. sparrmanii* does not have a horse-shoe shaped outline but conforms to the more usual U-shaped condition.

Vertebral numbers in the two species overlap (25–27 in *T. guinasana*, 26–28 in *T. sparrmanii*), although the modal number is lower (26) in former than in the latter (27).

In addition to marked differences in their live coloration, and the absence of polychromatism in *T. ruweti*, the latter species differs from *T. guinasana* in several other respects. Superficially, *T. ruweti* has a more slender body-form, a rounded dorsal head profile, and its caudal fin is distinctly rounded, more obviously so than in the few *T. guinasana* with a caudal margin approaching that condition.

The body scales in most specimens of *T. ruweti* are slightly smaller than in *T. guinasana* (26–28, mode 28 in the lateral series, cf. 25–28, mode 26 for the species respectively) as are those around the caudal peduncle (14–16, mode 15, cf. 12 in *T. guinasana*). There are, modally, more rows of cheek scales in *T. ruweti* (3, rarely 2, cf. 2, rarely 1 in *T. guinasana*); although in *T. ruweti* the lowermost scale row is not deeply embedded in the skin, it can easily be overlooked because it is almost completely overlain by the row above it. An unusual feature in the squamation of *T. ruweti* not shared with *T. guinasana* is the presence of a single scale between each of the lateral-line pores on the horizontal arm of the preoperculum; these scales are deeply embedded in the skin and are not visible without dissection. As compared with the scales in *T. sparrmanii*, especially on the body, those of *T. ruweti* have a more rugose central area, but the roughness is less marked than in *T. guinasana*, and the scales are also thinner and thus like those of *T. sparrmanii*.

Apart from the distinctly rounded caudal fin in *T. ruweti*, there are no other diagnostic features in the fins of the two species.

Gill-rakers in the outer series of the first gill-arch in *T. ruweti* are quite unlike those in *T. guinasana*, being finer and lanceolate, and having low and fine marginal serrations. The rakers are usually fewer in number (8 or 9) than in *T. guinasana* (8–10, rarely 11, mode 10).

When the neurocrania of comparable sized (ie. 47–65 mm S.L.) individuals are compared, the skull of *T. ruweti* is, in general, more like that of *T. sparrmanii* than that of *T. guinasana*, especially in the absence of any spongy hyperostosis of the frontals, and the absence of a ridge above or close to the cranial tubule linking the cephalic and infraorbital

lateral-line systems. Nevertheless, there are certain skull features resembling or approaching those developed in *T. guinasana*.

For example, the cephalic lateral-line tubules, except for that connecting the supraorbital pore with the main canal, are almost as indistinct, superficially, as are those of *T. guinasana*. Also, the area of the frontals between their lateral crests and the midline has a somewhat convex surface, albeit one less cambered than in *T. guinasana*, and the median frontal crest is as poorly developed as it is in comparable-sized individuals of *T. guinasana*.

The lower pharyngeal bone has proportions similar to those in *T. guinasana* (and *T. sparrmanii*), and its ventral surface shows a degree of bullation intermediate between that of the two species. The lower pharyngeal teeth are fewer and coarser than in *T. guinasana* (and also *T. sparrmanii*).

There are no specifically diagnostic features in the oral dentition of the two species, except that the lower dental arcade in *T. ruweti* does not have the near horse-shoe shaped outline characterizing the arcade in *T. guinasana*. The dentary itself is less bullate in *T. ruweti*, and the buccally directed mental thickening is not well developed.

Unlike *T. sparrmanii* but as in *T. guinasana*, the upper part of the subopercular posterior margin in *T. ruweti* has a distinct anterior inclination (see p. 31).

Based on figures given in Trewavas (1983) and a radiograph of 33 *T. ruweti* specimens from the Okavango delta, total vertebral counts in the two species overlap (26–28 in *T. ruweti*, 25–27 in *T. guinasana*), but the modal number is higher (27) in *T. ruweti*, than in the latter species (26), as is the modal number of abdominal centra (13 cf. 12 in *T. guinasana*). No epural fusion was noted amongst the Okavango *T. ruweti* radiographed.

DISCUSSION

The uniqueness of *T. guinasana*'s extensive, non-sexlimited polychromatism amongst tilapiine cichlids, indeed amongst any African taxon of that family, requires no further comment (see p. 22). Regrettably, nothing definite can be said about its evolution or its genetical basis.

It seems reasonable to assume that the founder population, whether it reached Lake Guinas by surface or subterranean means, was small and thus that the polychromatism may be a consequence of this and perhaps other genetical bottlenecks in its history. Since sexual dichromatism does not appear to be part of the specific mate recognition system (*sensu* Pater-son, 1985) in the genus *Tilapia*, there is, on that account, no reason why the alleles for different colour morphs should not spread through the population. Nor are there any obvious grounds for their being selected against or, for that matter, having a positive selective value (see p. 34).

Since polychromatism is known amongst other African and New World cichlids (Fryer & Iles, 1972; Greenwood, 1981; Barlow, 1976; 1983), albeit in a far more restricted way than in *T. guinasana*, its occurrence in that species is itself not exceptional, although 'aberrantly' coloured specimens of other *Tilapia* species have rarely been recorded. Indeed, the only published account I have found is of a blotched gold and black form of *Tilapia rendalli* from lake Kariba (Kenmuir, 1983: plate 32); unfortunately, no record is given of its

frequency in that lake. Nor has polychromatism ever been described from any populations of *T. sparrmanii*, including those occupying isolated sinkholes (eg. Wondergat in the Transvaal, RSA) or springs (such as Kuruman Eye, north-western Cape province and Molopo Oog, western Transvaal, RSA).

It has been suggested (Skelton, 1989) that '... this spectacular explosion of colour forms ...' in *T. guinasana* may be explained by the species, or its founders, having been present in a subterranean waterbody before it became a sinkhole. Consequently, '... in total darkness the genetic control over colour was lost'. Alternatively, Skelton (*op. cit.*) postulates that '... in the absence of competition or predation from other fish species, especially closely related species, there was little need or selection for a distinctive coloration for mate recognition, general communication or for camouflage purposes' (see also Penrith, 1978).

Because sexual dichromatism is not a characteristic of the specific mate recognition system in *Tilapia* species (see Trewavas, 1983), one of Skelton's four suggestions would seem to be negated. The existence of equally un-camouflaged colour morphs, and indeed brightly coloured breeding male cichlids in the clear waters of Lake Malawi, where predators abound (Fryer & Iles, 1972; Ribbink *et al.*, 1983), at first sight weakens any explanation based on selection for camouflaging coloration, although the absence of cover in Lake Guinas, when compared with Lake Malawi, could be a factor supporting Penrith's and Skelton's suggestion.

The importance of colour in communication, particularly at the interspecific level, is difficult to assess in the evolutionary and especially selectionist context under consideration. That it is important intraspecifically, at least for certain species, is well-established (see discussion in Fryer & Iles, 1972). It would seem in the case of *T. guinasana* adults that its role has been considerably diminished, but no research has been undertaken on that point. However, Ribbink (personal communication) did observe that in five of the principal colour forms, the coloration was expressed with different intensities and apparently related to differing emotional states. Those observations also appear to undermine Skelton's argument.

In the absence of any information on the genetical basis for polychromatism in *T. guinasana*, it is not possible to comment on Skelton's (*op. cit.*) views regarding polychromatism and the subterranean origin of the species, although in other cave or grotto-dwelling fishes (including a New World cichlid; Hubbs, 1938) the trend is towards loss or reduction of colour rather than an elaboration of patterns and pigments.

The other unique features of *T. guinasana* are concerned mainly with the cranial skeleton (see pages 27–30). In particular these involve the thickened and spongy nature of much of the frontals, the pitted and rugose ornamentation on those bones, the development of a ridge associated with the cephalic lateral-line tubule running into the infraorbital canal, and the inflated epiotic bone. Nothing approaching these features was seen in any of the other *Tilapia* species examined, nor were any found in the various *Oreochromis* and *Sarotherodon* species studied, which included all the taxa living in the thermal soda-lakes of East Africa (see Trewavas, 1983: 32–35).

In specimens of *T. guinasana* between 45 and 78 mm S.L., the somewhat inflated appearance imparted to the dorsicranium by the thickened frontals is enhanced by their generally convex rather than flat or even concave surfaces such as occur in comparable sized specimens of other species. This impres-

sion of a rounded or noticeably cambered surface in *T. guinasana* is reinforced by the fact that the cephalic lateral-line tubules, even in specimens larger than 78 mm, are sunken into the bone and do not break its surface contours. That condition, however, also occurs in *T. ruweti*, although it was not seen elsewhere in the genus.

The impression of a gently cambered dorsicranium in *T. guinasana* is less marked, however, when the largest skull (from a fish 135 mm S.L.) is compared with equal-sized neurocrania of *T. sparrmanii* (and other species, too). Furthermore, when comparisons are made between the skulls of small (ie. 41.0–45.0 mm S.L.) *T. sparrmanii* and those of *T. guinasana* between 45 and 78 mm S.L. it is apparent that, although the small *T. sparrmanii* skulls do not show any hyperostosis of the frontals, their dorsicrania have a cambered, gently convex appearance closely approximating to that of the *T. guinasana* skulls. Also, the *T. sparrmanii* skulls, when compared with those of larger conspecifics, show a proportional decrease in the height and extent of the median frontal crest, relatively lower fronto-parietal crests, and cephalic lateral-line tubules which are barely visible on the surface. In these characteristics the small *T. sparrmanii* skulls resemble closely skulls from larger *T. guinasana* specimens, although the curvature and generally domed appearance of the dorsicranium is more marked in the 45 mm *T. guinasana* than it is in the 45 mm specimens of *T. sparrmanii*.

This level of similarity between the skulls of small *T. sparrmanii* and those of considerably larger *T. guinasana* individuals suggests that, in many respects, the latter have retained, even into sexual maturity, the juvenile skull morphology of other tilapiines. The fact that the skull of the largest *T. guinasana* examined is more like that of a *T. sparrmanii* less than half its length, seems also to support the idea of delayed neurocranial morphogenesis in *T. guinasana*, at least with respect to the fish's standard length (the ages of the specimens being unknown).

To test that idea, the skull of a 38.0 mm S.L. *Tilapia zillii* (neurocranial length 10.5 mm) was compared with a *T. zillii* skull of 37.5 mm Nc.1 (from an individual of unknown standard length), and with skulls from *T. sparrmanii* 41.0 mm S.L. (Nc.1 11.0 mm), 80.0 mm S.L. (Nc.1 20.0 mm) and 92.0 mm S.L. (Nc.1 21.0 mm).

The areas of marked frontal cambering (and hence a domed appearance) in the small *T. zillii* skull (10.5 mm Nc.1) are almost identical with the similar-sized skull (11.0 mm Nc.1) of *T. sparrmanii*, but the median frontal crest in the former is lower, the cambering of the frontal medial to its contribution to the fronto-parietal crest is more pronounced, and the crest is lower. In those respects, the dorsicranium of the *T. zillii* skull is even nearer the usual adult condition in *T. guinasana* than is the similar sized skull of *T. sparrmanii*. When the dorsicrania of *T. sparrmanii* 80.0 and 92.0 mm S.L. (Nc.1 20.0 and 21.0 mm respectively) are compared with the largest *T. zillii* skull (Nc.1 37.5 mm), no obvious differences were noted, suggesting that in both species similar ontogenetic form-changes were involved, and that the skull in adult *T. guinasana* does retain certain features characteristic of much smaller individuals of *T. zillii* and *T. sparrmanii*.

Similar conclusions regarding ontogenetic changes in skull form were reached when the skulls in several alizarin preparations of laboratory spawned and reared *Oreochromis mossambicus* were compared with adults of the species and with the skulls of juvenile and adult *Tilapia sparrmanii*, *T. zillii* and *T. guinasana*.

In the small *O. mossambicus* (16.0–18.0 mm S.L.) the cambering of the dorsicranium is so pronounced that its entire dorsal surface could be described as domed. It is without traces of the gully between the supraoccipital crest and the region which will be occupied by the still undeveloped fronto-parietal crests, no or virtually no median frontal crest is present, and only the lateral-line tubule connecting with the infraorbital tubule is visible on the surface of the dorsicranium; the other cranial tubules, however, are faintly visible below the surface. In other words, the situation in these small *O. mossambicus* represents a more extreme form of that seen in *T. guinasana* 45.0–78.0 mm S.L. Since, in its overall appearance, the dorsicranium in adult and subadult *O. mossambicus* is closely similar to that in adult *T. sparrmanii* and subadult and adult *T. zillii*, one can conclude that all three species undergo similar ontogenetic form-changes which are not completed in *Tilapia guinasana* of a comparable size. The condition seen in the largest *T. guinasana* skull examined (neurocranial length 31.5 mm, from a fish 135.0 mm S.L.) suggests that even individuals of this size do not develop a skull-form free of juvenile features already lost in *T. sparrmanii* one third of their length.

One can, at present, only speculate on the causal, perhaps epigenetic, mechanism or mechanisms resulting in the *T. guinasana* condition. One such sequence of events may involve the hyperostosis and consequent thickening of the frontals constraining and influencing ontogenetic changes in the shape of the bones. Hyperostosis is manifest in the smallest wild-caught *T. guinasana* available, but in the absence of even smaller specimens its first appearance in ontogeny could not be ascertained.

If hyperostosis is involved, then an explanation is required for the seemingly restricted occurrence of the phenomenon, not only to *T. guinasana* but also its restriction to the scales and certain skull elements, in particular the frontals, part of the supraoccipital, the parietals and the epiotics of that species.

One possible explanation for the occurrence of hyperostosis in *T. guinasana* is that of environmental induction. Lake Guinas water has a very high calcium carbonate content (calcium hardness, as CaCO_3 , 185 ppm), an environmental factor to which the fishes might have responded, physiologically, by increasing the volume and calcification of certain bones. If that is so, the particular sites of hyperostosis (which also include the thickened scales; p. 25) still require explanation.

Without attempting to draw any conclusions on these issues, some observations on four laboratory spawned and raised *T. guinasana* may be relevant. The specimens are part of an F1 generation, derived from wild-caught parents kept, subsequent to their capture, in Grahamstown tap-water (calcium hardness, as CaCO_3 , ca. 45 ppm) in which the young were also raised.

In all four fishes the overall morphology of the dorsicranium is nearer that of similar sized wild-caught *T. sparrmanii* than of *T. guinasana*. The roofing bones involved (p. 27) are thinner and less spongy than in wild conspecifics, and there is a noticeable reduction in the pitting and rugosity of the frontals. The scales in these specimens, especially in the two larger fishes, are thinner and less rugose than in specimens from Lake Guinas, and the body of the lower pharyngeal bone is less bullate (p. 26). Interestingly, however, the morphology of the dentary, and the shape of its dental arcade (p. 30) are identical with those of wild-caught *T. guinasana*

and thus are noticeably different from the condition seen in *T. sparrmanii*.

It is planned to carry out, in the near future, experiments aimed at clarifying the extent to which such environmental factors as water chemistry may influence the structure of certain skull roofing bones and in turn influence the morphology of the dorsicranium in both *T. guinasana* and *T. sparrmanii*.

A close phyletic relationship between *T. guinasana* and *T. sparrmanii* was suggested by Trewavas (1936) on the grounds of both species having low numbers of gill-rakers, dorsal fin spines and scale rows on the cheek. On that basis, *T. ruweti* (Poll & Thys, 1965) could also be considered a close relative, the more so since it shares with *T. guinasana* certain features not found in *T. sparrmanii* (p. 33). However, because no fully cladistic phylogenetic analysis is available for the tilapiines it is impossible to assess the polarity of the features shared by the two taxa. Outgroup comparisons with other labroids and within the tilapiines (*sensu* Trewavas, 1983 but excluding the pelmatochromines and chromidotilapiines of Greenwood, 1987), strongly indicate that, on the basis of breeding habits and the nature of the pharyngeal dentition, the genus *Tilapia* is the most plesiomorphic member of the tilapiines (data from Trewavas, 1983; Thys, 1968, and personal observations). Within that genus, and because of their relatively coarse pharyngeal dentition with bicuspid teeth posteriorly on the lower bone, and their low vertebral numbers, *T. sparrmanii*, *T. ruweti* and *T. guinasana* are probably the least derived species (data sources as above). Within that trio of species, the unique polychromatism of *T. guinasana* (and possibly its unusual osteological features) give it a derived status, as do certain features of *T. ruweti* (see p. 33), whilst *Tilapia sparrmanii*, with its generalized syncranial osteology seems to be the most plesiomorphic form.

There is some doubt about the genetic rather than ecophenotypic basis for certain of the apparent osteological autapomorphies characterizing *T. guinasana* (see discussion above), but no doubt can be entertained about the uniqueness of its polychromatism.

Unequivocal synapomorphies shared by *T. guinasana* and either *T. ruweti* or *T. sparrmanii* cannot be identified at present. Consequently, sister species are unidentifiable and the presumed close relationship between *T. guinasana* and *T. sparrmanii* can only be considered conjectural. The overall superficial similarity between the two species has also led to arguments, mostly unpublished, that *T. guinasana* should not be treated as a distinct species, but rather as a variant population of *T. sparrmanii* (see discussion in Skelton, 1988).

As with all disjunct populations there is no adequate way of establishing the existence, or otherwise, of intrinsic barriers to successful genic exchange between *T. guinasana* and *T. sparrmanii*, and thus determining their status as biological species. On the other hand, the apparently absolute physical isolation of *T. guinasana*, taken together with the autapomorphic characters it exhibits, qualify it for the status both of a phylogenetic species (*sensu* Cracraft, 1989) and of an evolutionary species (*sensu* Wiley, 1981). Thus in my view, its specific status cannot be doubted, a conclusion also reached by Oosthuizen *et al.*, (1991) on the basis of their biochemical studies.

APPENDIX

Tilapia guinasana in Lake Otjikoto

The first transfer of *T. guinasana* to Lake Otjikoto, another sink-hole lake with similar water chemistry, some 50 km east of Lake Guinas, is recorded as taking place in 1922, (see p. 21) but it may not have been successful since, when Jordan's party visited the lake in 1931 and collected fishes there, no *T. guinasana* were included amongst the material studied by Trewavas (1936); see also Penrith (1978); and Skelton (1988; 1989). However, the species is now well established in the lake.

Only four preserved specimens of Otjikoto *T. guinasana* were available for study; all are adults in the size range 74.5–86.0 mm S.L. A cranial skeleton was prepared from the 75.5 mm specimen.

In all morphometric and meristic features, these specimens lie within the ranges for fishes from Lake Guinas, and in no morphological or dental features, including the shape of the dental arcade of the lower jaw (see p. 30), do they differ from the parental stock. However, the Otjikoto individuals all have a circumpeduncular scale-count of 13, a figure rarely recorded from the Guinas sample, and the rugosity of their body scales is less marked.

The skull shows no clear-cut departure in its gross morphology from those of Guinas specimens, although the frontal rugosities and pitting are less pronounced and fewer in number.

It is not possible to determine live colours from the preserved material, but Dr Ribbink and Ms Twentyman-Jones (personal communications) have seen representatives of the light blue and olive morphs, and a striped form, when diving, in poor visibility, in Lake Otjikoto.

ACKNOWLEDGEMENTS. It is with great pleasure and a deep sense of indebtedness that I thank Tony Ribbink and Vanessa Twentyman-Jones for all they have contributed to this paper. Not only am I grateful for their meticulously preserved and documented collection of fishes, their acute observations and constant willingness to provide information about the lake and its fishes but, and in particular, for their unflagging enthusiasm and encouragement as well as for introducing me to the fascinating problems posed by the 'Guinas cichlids'. To Tony Ribbink go my thanks for his critical reading of the manuscript and his helpful comments.

As usual, Paul Skelton, also of the J.L.B. Smith Institute, has proved an invaluable sounding-board for ideas, and was always ready to discuss the detailed and broader issues involved in this study. Rob Stobbs exercised great skill in producing radiographs, and Huibre Tomlinson even greater tolerance and patience in preparing the typescript. To them all, my profound thanks, which also go to Elaine Heemstra for so skillfully exercising her artistic talents when producing Figure 1, a trying task beautifully executed, and to Chris Jones and Phil Crabbe of the N.H.M.'s E.M. Unit and Photographic Department respectively, for the photographs.

Finally, my thanks to the Director of the J.L.B. Smith Institute, Mike Bruton, for his hospitality and help in many other ways.

REFERENCES

- Barlow, G.W. 1976. The Midas cichlid in Nicaragua. pp. 333–358. In: Thorson, T.B. (Ed.) *Investigations of the Ichthyofauna of Nicaraguan Lakes*. University of Nebraska Press. Lincoln.
- Barlow, G.W. 1983. The benefits of being gold: behavioral consequences of polychromatism in the Midas cichlid, *Cichlasoma citrinellum*. *Environmental Biology of Fishes*, 8: 235–247.
- Cracraft, J. 1989. Speciation and its ontology. pp. 28–59. In: Otte, D. & Endler, J.A. (Eds) *Speciation and its Consequences*. Sinauer Associates Inc. Massachusetts.
- Fryer, G. & Iles, T.D. 1972. *The Cichlid Fishes of the Great Lakes of Africa*. T.F.H. Publications. Neptune City.
- Greenwood, P.H. 1981. *The Haplochromine Fishes of the East African Lakes*. 839 p. Kraus-Thomson Organization GmbH. Munich.
- Greenwood, P.H. 1986. The *pars jugularis* and the intrarelationships of cichlid fishes (Labroidei; Teleostei). *Journal of Natural History* 20: 949–974.
- Greenwood, P.H. 1987. The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. *Bulletin of the British Museum (Natural History)*, Zoology 53 (3): 139–203.
- Hubbs, C.L. 1938. Fishes from the caves of Yucatan. *Publications Carnegie Institution of Washington*. No. 491: 261–295.
- Jubb, R.A. 1967. *Freshwater Fishes of Southern Africa*. vii + 248 p. Balkema. Cape Town.
- Kenmuir, D. 1983. *The Fishes of Kariba*. iv + 131 p. Wilderness Publication. Harare.
- Oosthuizen, S., van der Bank, F.H. & Ferreira, J.T. 1991. 'n Biochemiese en morfologiese ondersoek van *Tilapia guinasana*, *T. rendalli* en *T. sparrmanii*. *Suid-Afrikaanse Tydskrif vir Natuurwetenskap en Tegnologie* 10, no. 1: 56.
- Paterson, H.E.H. 1985. The recognition concept of species. pp. 21–29. In: Vrba, E.S. (Ed.) *Species and Speciation*. Transvaal Museum Monograph (4). Pretoria.
- Penrith, M.J. 1978. Otjikoto Lake. *South West Africa Annual*, 1978: 138–139.
- Poll, M. & Thys van den Audenaerde, D.F.E. 1965. Deux Cichlidae nouveaux du Sud du Bassin du Congo. *Revue de Zoologie et de Botanique Africaines* 72: 322–333.
- Ribbink, A.J., Marsh, B.A., Marsh, A.C., Ribbink, A.C. & Sharp, B.J. 1983. A preliminary survey of the cichlid fishes of rocky habitats in lake Malawi. *South African Journal of Zoology* 18: 149–310.
- Ribbink, A.J., Greenwood, P.H., Ribbink, A.C., Twentyman-Jones, V. & van Zyl, B. 1991. Unique polychromatism of *Tilapia guinasana*, an African cichlid fish. *South African Journal of Science* 87: 608–611.
- Skelton, P.H. 1988. Freshwater fishes of South West Africa. *Roan News; The Wildlife Society of S.W.A.* 1/88: 1–5.
- Skelton, P.H. 1989. Gems of a different kind. *Rössing, October*, 1989: 6–11.
- Skelton, P.H. 1990. The status of fishes from sinkholes and caves in Namibia. *Journal of the Namibia Scientific Society* 42: 75–83.
- Thys van den Audenaerde, D.F.E. 1964. Revision systematique des especes Congolaises du genre *Tilapia* (Pisces, Cichlidae). *Annales, Musee Royal de l'Afrique Centrale, Tervuren. Serie in 8°, Sciences Zoologique*, No. 124: 1–155.
- Thys van den Audenaerde, D.F.E. 1968. An annotated bibliography of *Tilapia* (Pisces, Cichlidae). *Documentation Zoologique No. 14, Musee Royal de l'Afrique Centrale, Tervuren*: xl + 406.
- Trewavas, E. 1936. Dr Karl Jordan's expedition to South-West Africa and Angola: The fresh-water fishes. *Novitates Zoologicae, Tring* 40: 63–74.
- Trewavas, E. 1973. I. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. *Bulletin of the British Museum (Natural History)* Zoology 25(1): 1–26.
- Trewavas, E. 1983. *Tilapiine Fishes of the Genera Sarotherodon, Oreochromis and Danakilia*. viii + 583 p. British Museum (Natural History). London.
- Vanderwalle, P. 1973. Ostologie caudale des Cichlidae (Pisces, Telcostei). *Bulletin biologique de la France et de la Belgique* 107: 275–289.
- Wiley, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. xv + 438 p. Wiley. New York.